

The Acidity of Muscle during Maintained Contraction.

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In 1913, I described a method for recording changes in hydrogen-ion concentrations in tissues, by means of a manganese dioxide electrode in combination with a calomel electrode (1). By this method it was shown that the acidity of muscle probably increased at the same time as, or slightly before, the tension increased, and that the acidity decreased as the muscle relaxed (2).

In a paper, which appeared as this note was being prepared for publication, Ritchie* states that he has been unable to detect a variation in acidity by the use of manganese dioxide electrodes. I am inclined to think that his failure is due to the injury to the muscles on insertion of wires into its substance. In my own experiments the wires rest on the surface of the muscle.

The electrical change observed by me is not due to spread of potential from the stimulating circuit, because in some records a potential is recorded corresponding to the time of stimulation. This potential is quite separate from the larger potential ascribed to the acid production, and it may be in the same or in an opposite direction from that which accompanies the contraction.

In my experiments I took precautions to minimise movement of the electrode on the surface of the muscle, and any slight movements are probably less important with the sartorius than with the gastrocnemius. Change of potential, due to movement of the electrode, would probably vary in direction, whilst with the manganese dioxide electrode the change is always in the same direction. If the electrode did move on the surface of the muscle it is unlikely that the potential would return to its former value, as it is seen to do in most of my records.

Other forms of metallic electrodes would give changes of potential depending on the chemical reactions that take place in contact with them.

I do not think that the change shown by a manganese dioxide electrode is due to polarisation. If the electrodes are so placed that no difference of potential is shown during contraction by non-polarisable electrodes, it is difficult to see how any difference of potential will be produced when one calomel electrode is substituted by a manganese dioxide electrode and the

* A. D. Ritchie, 'Journ. Physiol.,' vol. 56, p. 53 (1922).

contact potential has been properly balanced. If there is no difference of potential there cannot be any current, therefore there will be no polarisation.

If acidity is related to tension in muscle it is necessary to show that acidity remains when the muscle tension is maintained, and decreases when the tension falls. In order to test the relation of acidity to muscle tension two experimental procedures were tried.

In the first, veratrin was painted on the frog's muscle after a record of the normal contraction had been made. The out-standing feature of the action of veratrin is that it does not affect the increase in tension of the muscle, but that it delays the relaxation.

With such a preparation the acidity, as shown by the manganese dioxide electrode, remains also. Fig. 1 shows a muscle twitch of a fresh sartorius, whilst fig. 2 shows the result with the same muscle after it had been treated with veratrin ($1:10^5$).

For the second procedure a decerebrate cat was used. This preparation shows a marked tension (decerebrate rigidity) in the limb muscles. The tension can be abolished by cutting the efferent nerves to the muscles, or by reflex inhibition as the result of stimulation of an afferent nerve.

In decerebrate preparations the rigid muscles show a greater acidity than when the muscles are paralysed by cutting their efferent nerve supply, as shown by the following results:—

Table I.—Decerebrate Preparations showing Potential in Volts between a Manganese Dioxide Electrode and a Calomel Electrode.

Date.	<i>R. Sartorius.</i>			<i>L. Sartorius.</i>		
	Rigid.	After cutting nerve.	Difference.	Rigid.	After cutting nerve.	Difference.
21.7.13 ...	0·325	0·004	0·321	0·186	—0·169	0·355
14.7.14 ...	0·312	0·249	0·063	0·249	0·242	0·007
8.3.21 ...	0·355	0·206	0·149	0·866	0·771	0·095
	Average		0·178	Average		0·152

Although the absolute values of these are unreliable it is clear that paralysing the muscle always gives a result corresponding to a decrease in acidity.

In order to demonstrate further that removal of maintained contraction causes decrease in acidity, a reflex vasto-crureus preparation was used (3). The sartorius was removed and the electrodes placed on the surface of the vasto-crureus. On causing a reflex inhibition by stimulation of the ipsilateral

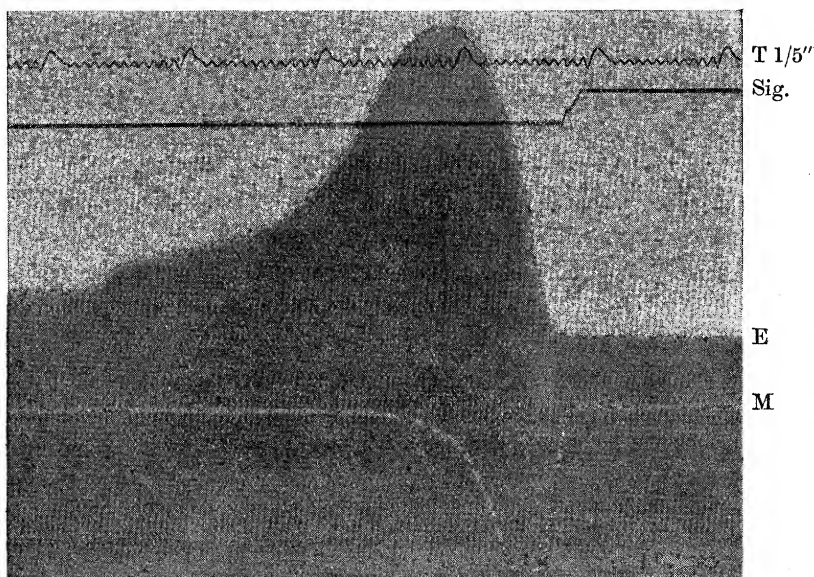


FIG. 1.—Simple muscle twitch.

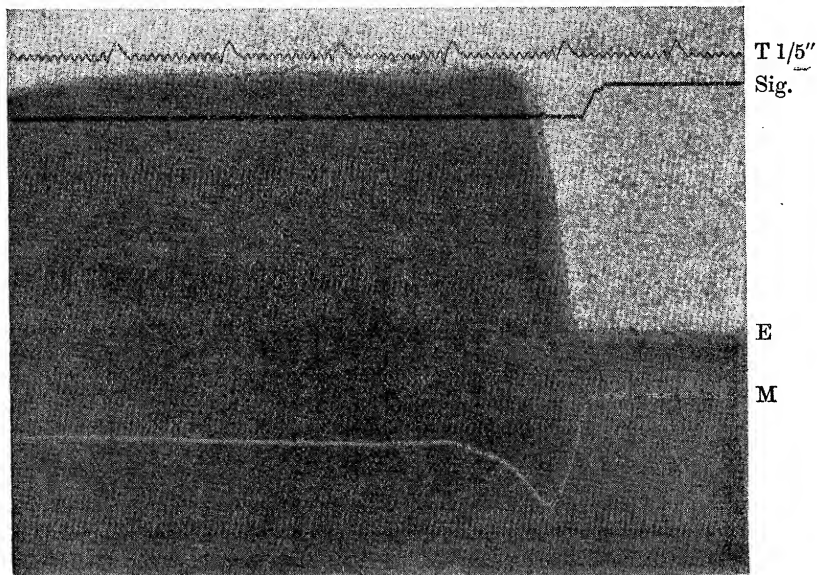


FIG. 2.—Record of same muscle after treatment with veratrin ($1:10^5$). Records read from right to left. Top line, time in $1/5''$. Second line, signal for single break-shock given to muscle. Bottom line, downward movement shows increased tension by muscle. Shadow shows movement of mercury in capillary. Movement upwards corresponds to increased acidity at manganese dioxide electrode.

sciatic nerve, as shown in fig. 3, the end result corresponds to a decrease in acidity. The initial result is still doubtful, as the figure reproduced shows a movement of the mercury in the opposite direction before the inhibition occurs. This result may be due to either a slight contraction before relaxation,* or setting free of acid from the muscle preliminary to its removal by some other mechanism.

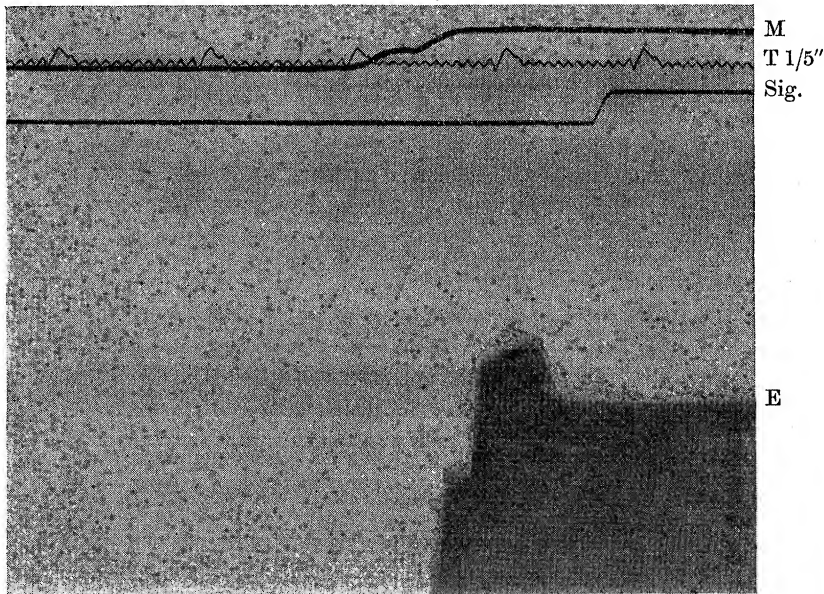


FIG. 3.—Record of reflex inhibition. Indications as in figs. 1 and 2, but relaxation of muscle is shown by a line which starts above time marker and falls across it, instead of the record of contraction shown below. Relaxation is accompanied by decrease in acidity.

The results indicate that acidity and tension in muscle are concurrent. Thus it may be better to investigate, not how the contraction is maintained, but why the acid remains and is not removed as in a simple twitch. The results further suggest that as acidity is common to both tetanus and tone probably the mechanism for the production of both is the same, *i.e.*, that there is one mechanism in muscle and not two.

I wish to thank Mr. F. C. Smith for assistance in some of the experiments on decerebrate cats. Some of the apparatus for the research was obtained

* Sir Charles Sherrington informs me that weak reflex inhibition is frequently preceded by a slight contraction. This fact is in favour of the view that the slight increase in acidity, shown before relaxation occurs, is due to a preliminary increase in tension.

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- (1) H. E. Roaf, 'Roy. Soc. Proc.,' B, vol. 86, p. 215 (1913).
- (2) H. E. Roaf, 'Journ. Physiol.,' vol. 48, p. 380 (1914).
- (3) C. S. Sherrington, "Mammalian Physiology," 'Clarendon Press,' Oxford, 1919, p. 117.

On the Heat Production and Oxidation Processes of the Echinoderm Egg during Fertilisation and Early Development.

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Introduction.

In the following experiments an attempt is made to measure the heat liberation of the ovum on fertilisation and early development, and to correlate this with the amount of oxygen consumed and the carbon dioxide given off at the same time. New methods hitherto unused for this purpose have been employed. The question has already been investigated by Meyerhof (1) in an extensive paper published in 1911. He determined the heat production and the oxygen consumption of the egg of the sea-urchin *Strongylocentrotus* on fertilisation and early development. The heat production was measured directly by means of a finely divided Beckmann thermometer, while the eggs were contained in a small closed vacuum flask completely submerged in the water of a carefully regulated thermostat. The oxygen consumption of the eggs was at the same time determined at intervals of an hour, by the titration of the sea-water in which the eggs were kept with sodium thiosulphate by the Winkler method.

The heat given off by a known quantity of eggs expressed in gram calories per hour, divided by the amount of oxygen consumed in the same time expressed in milligrams, gave him a calorific quotient which he calls "Q." This he found for the early stages of segmentation to be about 2.75, but if the heat of solution of carbon dioxide to form bicarbonate with the sea-water is taken into consideration this value becomes 2.6. This figure is

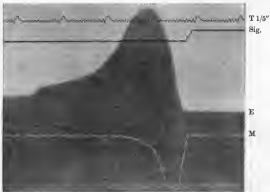


FIG. 1.—Simple muscle twitch.

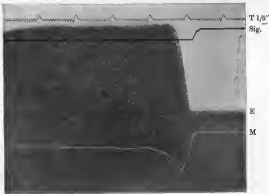


FIG. 2.—Record of same muscle after treatment with veratrin ($1:10^6$). Records read from right to left. Top line, time in $1/5\%$. Second line, signal for single break-shock given to muscle. Bottom line, downward movement shows increased tension by muscle. Shadow shows movement of mercury in capillary. Movement upwards corresponds to increased acidity at manganese dioxide electrode.

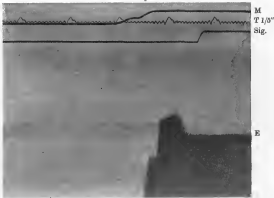


FIG. 3.—Record of reflex inhibition. Indications as in figs. 1 and 2, but relaxation of muscle is shown by a line which starts above time marker and falls across it, instead of the record of contraction shown below. Relaxation is accompanied by decrease in acidity.